EVALUATING THE EFFECTS OF MANAGEMENT ON TERRITORIAL POPULATIONS USING SWARM

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Abstract. For centuries, coyotes have been controlled to protect livestock and/or enhance game populations. The intensity of control has varied widely and many types of control techniques have been used. The effects of these control techniques need to be evaluated to effectively resolve conflicts among agencies and interest groups, to fulfill legal requirements, and to aid the development of new strategies for managing populations. However, the influence of these techniques on coyote population size and structure is largely unknown. Furthermore, management decisions are often required before experimental tests can be developed and conducting requisite experimental programs on meaningful scales are logistically prohibitive. Therefore, we developed an individual-based computer model using Swarm to evaluate the effects of various control techniques on age structure including selective removal, random removal, and denning. This model is part of a larger effort to fully evaluate the effect of current management strategies on coyote populations and to eventually link this population model to a depredation model. Selective and random removal resulted in younger age structures, whereas denning produced population age structures similar to an unexploited population.

Key words: computer model, control techniques, coyote, Canis latrans, individual-based model, population, Swarm.

INTRODUCTION

Resolving livestock depredation conflicts efficiently and effectively is the goal of various public and private agencies. However, these situations are frequently confounded by conflicting values associated with various interest groups. At such times, accurately projecting the likely outcomes from alternative management techniques becomes important in assessing the relative merits of differing approaches. Frequently, decisions are required before experimental results can be developed. In addition, conducting requisite experimental programs on meaningful scales are logistically prohibitive. Acquiring cooperation for experimental approaches among private enterprises can be difficult, especially where personal livelihoods are at stake or where there are only meager assurances the management techniques might be effective. At the same time, there is a need to project likely outcomes of various management strategies to (1) fulfill legal requirements associated with the National Environmental Policy Act of 1969 as amended (Public Law 91-190, 42 U.S.C. §§ 4321 et seq.; 83 Stat. 852), (2) identify procedures most likely to provide efficient and effective resolution of problems within existing socio-political constraints, and (3) provide guidance in the process of identifying new approaches for resolving problems.

Developing computer models that incorporate the biological, legal, ethical, and socio-political aspects of management programs is one approach. We are initiating such a process as it applies to resolution of coyote depredation problems, with an initial goal of developing a coyote population model that incorporates our current understanding of the factors and mechanisms associated with regulating coyote density. Ultimately, this portion of the model will incorporate environmental aspects such as prey availability, inter-specific competitions and aggressions, and perhaps topography and climate. The immediate goal, however, is to develop a program that realistically depicts natural functions of coyote populations with a variety of "windows" whereby ramifications associated with changes in reproductive and mortality patterns can be explored. The purposed of this part of the model was to evaluate the influence of various control techniques on population age structures.

A previous coyote population model (Connolly and Longhurst 1975) required multiple assumptions of coyote demographic parameters to implement the model, like most animal population models developed thus far. Our current understandings of coyote population functions, however, involve two important behavioral aspects that were not understood at the time of the Connolly and Longhurst's (1975) effort. The first involves the number of coyote social units that exist within any given area because a geographic space is strongly defended. The second, social dominance hierarchies, appears to limit the number of individuals within individual social units, as well as the number of reproductively active females. As a result, the functional unit within coyote populations is the social unit, rather than the individual as most demographic models assume. The existence of multiple potential breeders within populations creates resilience not commonly recognized in many modeling techniques. To accommodate these aspects, we chose to model coyote populations on the basis of social units. Individual animals are still recognized to have independent probabilities of life and death, as well as the ability to move into and out of the reproductive portion of the population. The constraints associated with territoriality and social dominance place stringent limits on the productivity, but also provide a resounding resilience to the population.

We developed a computer model to evaluate the effects of various control techniques on age structure. We hypothesized that selectively or randomly exploited populations would have younger age structures, low adult survival, high reproductive rates, and high recruitment into the adult population (Knowlton et al. 1999). Whereas populations that were exploited by denning would have age structures, adult survival, and recruitment similar to unexploited populations.

METHODS

To analyze the effects of various management techniques, we built an individual-based computer model using the Swarm modeling system. Swarm is a software platform that consists of a set of libraries of objects (i.e., a list of functions or routines), schedules, display functions, and hierarchical structures that facilitate implementation of individual-based models (Minar et al. 1996, Savage and Askenazi 1998, Daniels 1999). Swarm was chosen because the system allows the user to describe individual behaviors one by one for all individuals, link those behaviors in a concurrent time step, and build behaviors and objects in a hierarchical framework. To take advantage of these Swarm features, we wrote the program in Objective C, a dynamic object-oriented language. Dynamic languages place actions into objects (e.g., individuals) instead of placing actions into variables that hold the objects as others commonly do. Thus, individuals are able to move or act independently from each other as they move through life (Carnahan et al.1997, Railsback et al. 1999). The basic structure of the Swarm model is a series of linked files that describe different objects in the modeling space or world. The modelswarm describes the world and declares what objects (e.g., animals) it will contain. In our modelswarm, we have a terrestrial landscape with packs of coyotes and a management function that removes coyotes. Other files contain the details that describe objects and actions, such as the list of coyote packs, who is in each pack, and what happens in a monthly time step as a coyote ages from birth through death.

Although individual coyotes are modeled, the model structure is pack based. For example, breeding, socializing, and available resources depend upon the particular pack membership. Individual coyotes in the model are labeled according to age, weight, sex, pack affiliation, and status (i.e., alpha, beta, and young). Coyotes socialize (i.e., attempt to move up in status), breed, die from natural causes, or be removed by the management function as the model moves in monthly time steps. Initial population structure (e.g., age, mortality, etc.) was taken from unexploited coyote populations in Idaho, Utah, Texas (Knowlton 1972; F. F. Knowlton unpubl. data, USDA, APHIS). The probability of natural mortality during any one month was based upon a linear relationship between pack size and mortality (i.e., density dependent mortality). Each month, the probability of natural mortality within a pack was calculated by multiplying the number of individuals in a pack by 0.005 (Knowlton 1972; F. F. Knowlton unpubl. data, USDA, APHIS). We determined the annual number of offspring produced per alpha female (3.73 ± 2.1) based on an 8-year data set from 24 pairs of captive coyotes (J. Green unpubl. data, USDA, APHIS, WS).

In addition to natural mortality sources, coyotes can be removed from the population according to a management function. The management function is designed to remove animals based on their age and status (Knowlton et. al 1999). Selective control removes specific animals based on their age or status (e.g., such as the alphas with calling and shooting). Random control removes animals at random but is limited to adult animals (e.g., random trapping or aerial gunning). Denning removes all of the offspring (< 2 months of age) within a pack. The pack is selected at random and the number of offspring removed is not known at the time of the action. Furthermore, removing specific individuals can effect the survival of others. For example, offspring are linked to a specific female, so by removing the female from the population all of her offspring will also die when the offspring are young (< 2 months). The number of animals removed and the technique used can vary from month to month according to user input as prompted by the model.

We ran the model for 10 years using no removal, selective removal only, random removal only, and denning only. Using selective and random control, 1% of the initial adult population was removed each year. Selective control removed only the alphas. We removed 4% of the dens each year with an average of 3 young per den. We ran each model for 20 iterations effectively producing 20 populations. We then compared age structure and population size among the control techniques at the end of the 10-year period. Age structures, average age, and population sizes were compared among techniques using a one-way ANOVA (Zar 1999). Although this part of the modeling program was not designed to evaluate the effect of control on population size, we include this analysis here to provide additional information for the age structure analysis and a preliminary indication of effects.

Results

The four treatment structures produced significant differences in population structure and size (Figure 1). Removing 4% of the dens each year resulted in an older age structure, whereas selectively or randomly removing adults resulted in younger age structures ($F = 194.7$; df = 3, 56; $p < 0.0001$). Denning removed 2 - 8% of the total population annually depending on the number of young associated with each reproductive pair. The denning control resulted in an older average age compared to the no control treatment control ($F = 4.85$; df = 3, 76; $p = 0.004$). Comparatively, the random or selective removal of adult animals from populations resulted in younger average age when compared to the no control treatment. Population size varied from 70 – 88 animals according to control technique. Removal using denning resulted in 13% smaller populations sizes than those exposed to other control techniques ($F = 3.45$; df = 3, 76; $p = 0.021$). All of the populations continued to grow during the 10-year analysis period (e.g., no population became extinct).

DISCUSSION

We expected a shift to younger population age structures for random and selective control

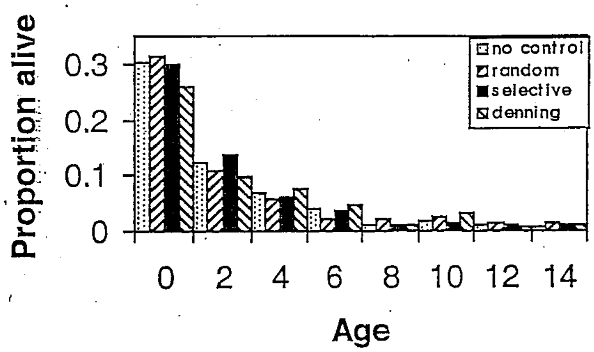

FIGURE 1. Computer model projections of the proportion of coyotes alive after 10 years of exposure to various control techniques: no control, selective removal of alpha males and females, and removal of a litter.

Denning, however, resulted in an older population structure and higher average age. This change in structure was due to a decrease in the number of young (< 1 year) animals. As a result of the model using density dependent mortality, the removal of young animals in a pack produced lower mortality probabilities for older animals. The probability of natural mortality was inversely related to the number of individuals in a pack. Hence, the removal of younger animals reduced pack size, thus reducing the probability of natural mortality.

Control had little effect on population size for most populations because they were subjected to low levels of control that simulated removal practices used to protect livestock.

Denning led to lower population sizes, but the proportion removed was larger (e.g., 8%) than that removed with selective or random removal (e.g., 1%). Smaller population sizes could occur with selective and random removal if they removed proportions similar to those removed by denning.

because these control methods increase the mortality for adult animals. It is likely that the selective removal of individuals has a stronger effect on age structure than random removal because it targets the older, more dominant animals while random removal does not distinguish between alphas and betas.

These modeling results may be useful in managing coyote populations, reducing depredations, modifying techniques, or providing effects analysis for these control techniques. Older coyotes may have reduced reproductive rates compared to younger animals (J. Green unpubl. data, USDA, APHIS, WS). Lower reproductive rates may lead to smaller population sizes. Furthermore, depredation on livestock may be more likely when coyotes are provisioning young, consequently a lower reproductive rate may reduce depredation events (E. Gese unpubl. data, USDA, APHIS, WS). Conversely, the lower age structures resulting from selective and random control may increase depredation rates because younger coyotes may have a higher reproductive rate, but this remains to be verified with field data or a more complete model. In addition, younger animals may be more prone to these removal techniques and thus this negative effect may be largely avoided. Using these low but realistic control levels, selective and random removal did not greatly (< 0.5 year) alter average age in populations.

Although this structural model was not designed to test this explicitly, population size was not effected by low levels of removal using random or selective control. However, more investigation is needed to determine the level of control needed to reduce population size. Nonetheless, it was possible to demonstrate the resistance of territorial populations with this fairly simple population structure model. To accurately assess effects of various control levels on population size, more elaborate models and detailed analysis is needed.

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